# ON THE STUDY OF ZOOGEOGRAPHICAL REGIONS BY MEANS OF SPECIFIC CONTOURS.

## WITH AN APPLICATION TO THE *ODONATA* OF AUSTRALIA.

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(Plate i., and Transparencies 1-3.)

It can scarcely be denied that the science of Zoogeography is in a somewhat unsatisfactory condition, and that great difficulties exist both in the following out of lines of research and in the drawing of general conclusions. This is not to be wondered at, when we realize that the present distribution of the fauna and flora of the earth has been brought about by the acting together of so many conflicting conditions, continually changing throughout immensely long geological periods; and that the task of re-picturing or re-constructing these conditions is in itself a most baffling one, owing to the very fragmentary evidence still preserved to us.

Under these circumstances, any method which may promise to yield good results, and to give us a clearer view of the problem in hand, is worthy of a trial. The author, therefore, offers the method explained in this paper, with the intention neither of ousting any of the already approved methods of study, nor of proclaiming the discovery of a panacea for the difficulties known to exist; but rather with the purpose of presenting the subject in a new light, in which, it is hoped, certain facts may be made to stand out in bolder relief than they have hitherto done.

It is now generally admitted that the six main zoogeographical regions, as originally proposed by Sclater, and modified by Wallace, are valid subdivisions of the land-surface of the earth, as far as its fauna and flora are concerned. But though these

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regions may be marked off very definitely in the case of certain groups—as, for instance, in the case of the Mammalia and the Passerine Birds, for which they were originally instituted—yet in other cases the boundaries between them may be more or less transgressed, or may even be non-existent for certain groups. This is, of course, due to the fact that the barriers which mark off the different regions may not always have been barriers in time past, nor may they be complete barriers in time present. It can be easily seen, for instance, that Wallace's line need not prove a bar to the migration of strong-flying insects, nor need the arid tract that somewhat vaguely separates the Nearctic from the Neotropical Region be any bar to the progress of eremian forms of animals or plants.

It is no wonder, therefore, that much less agreement should be found amongst the opinions of students when we come to consider the question of *subregions*. Many schemes have been proposed for the subdivision of the six main regions into subregions of approximately co-ordinate value. Possibly the desire for uniformity and symmetry has been one of the underlying forces in some of these attempts. One scheme, with a good deal to recommend it,* divides each main region into four subregions. Such divisions cannot, however, be regarded as of co-ordinate value. To take an example, the Australian region is subdivided into the Australian proper (Australia and Tasmania), the Papuan, the Polynesian, and New Zealand (with its allied islands). Of these, New Zealand stands in a higher rank than the others, and is claimed by many scientists to form actually a separate region. On the other hand, the division does not recognise the claims of the South-Western corner of Australia, which, to botanists at any rate, will appear to be as distinct a subregion as could possibly be found; while, on the other hand, the so-called Polynesian subregion is founded purely on negative characters, and is only doubtfully to be included in the Australian region at all.

The present paper is an attempt to approach the subject from a different view-point. The desire to draw hard-and-fast divisions exaggerates the actual boundaries reared by Nature at

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* Text-Book of Zoogeography, F. E. Beddard.

various times and in various manners, and we are apt to lose
sight of the great fact of the underlying unity of descent con-
necting together the various groups of animals or plants upon
the earth. In the method proposed, no attempt will be made to
indicate *land-area* divisions or subdivisions; but the attempt at
subdivision or classification will be devoted to the *actual contours
of groups*. The construction of these contours is, however, a
matter of great difficulty. As the author is convinced of the
futility of attempting such a task, except under the guidance of
very strict and definite rules, the following scheme is here pre-
sented as an explanation of the method, for which the name
"*Method of Specific Contours*" is proposed :—

### i. Selection of the Land-Area.

Any land-area, either continuous or discontinuous, may be
selected *which may be considered to have claims to be regarded as
a zoogeographical unit*. Without doubt the best results will be
obtained by the drawing of contours over the complete area of
one of the six main zoogeographical regions. For the study of
circumpolar or circumtropic distributions, it would be advisable
to take the total land area of the earth into discussion. Parts
of a region (such as Madagascar, New Zealand, or Australia with
Tasmania), may be studied separately with good results, provided
the unity of the prevailing flora or fauna of a region is not
destroyed by the selection of an area that has no claims to be
considered as a unit.

### ii. Selection of the Group.

The group of animals or plants selected for study by contours,
whether it be a single genus, group of genera, subfamily, or
division of higher order, *must be a natural group clearly marked
off from its nearest allies*. Genera or other groupings merely
based on taxonomic expediency cannot be used. For if we fail
to take into account any portion of a complete natural group,
we cannot expect to obtain a completely natural result. In
particular, *known* convergences of type must be carefully avoided;
but, on the other hand, when convergence is not yet proved, the
resulting contour may give valuable evidence as to its existence,

### iii. Collection of Records.

It is essential that the records used be *fairly complete.* Pro-
bably in very few cases can the complete records of distribution
of even a single species be obtainable. But this is not necessary,
because the object of the method is not to produce contours of
impeccable accuracy (such, indeed, are practically an impossi-
bility), but to study the *type* of contour produced. The altera-
tion of a contour line a few miles (or even perhaps a few hundred
miles) usually will not affect our ability to recognise it as belong-
ing to a particular type. As an example of the kind of contour
aimed at, one may offer any of the well-known meteorological
contour maps drawn over a large area. In these, the *general*
distribution of isobars, isohyets, or isothermals, is very clearly
shown; but these lines are drawn as free curves, and ignore
many small local variations. To give a good example, the
average annual rainfall map of Australia (Plate i.) is produced
from about *seven hundred* records. Doubtless, if we could have
access to *seven thousand* records, a much closer approximation to
the truth could be obtained. Yet nobody would seriously main-
tain that the contour as now produced is not accurate enough for
all practical purposes, *especially for study as a complete whole*, in
which too much attention to detailed curvings of contour-lines
would mar the clear effect now obtained.

Under this heading, it is hoped that the method of Specific
Contours will, if adopted, lead to a closer recognition of the *value
of every single record* that can be obtained *of every single species,
however common it may be.*

### iv. The validity of Species.

No attempt can here be made to answer the question "What
is a species?" To each student who desires to use the method,
sufficient common sense may be attributed not to mar the result
by an insistence on the recognition, as species, of units of lower
than specific value. In this connection, it should, however, be
clearly noted that, on the whole, both "splitter" and "lumper"
will produce approximately the same contours for a given group.
For, if a recognised species, A, be subdivided into any number of

species, $A_1$, $A_2$, $A_n$, the contour will not be affected *unless two or more of the forms occur in a single locality.* But as nearly all the argument between " splitters " and " lumpers " occurs about " geographical races," it follows that in such cases no alteration of the contour is effected by a change of opinion, since the species in question *can only score "one"* in each locality in which it occurs.

Local varieties, known to be produced as the offspring of a definite species, should on no account be included as " species."

### v. Application of the Method.

On the map of the area to be studied, each locality from which records are obtainable should be marked down. Against each, the *number* of species (of the group in question) occurring in that locality should be written. Contour lines are then to be drawn as *free curves enclosing in turn all those localities possessing the same number of species.* In the simplest cases (where no lacunæ or breaks occur), the result will be as follows : —

Between the outermost contour-line (1) and the next (2) will lie all those localities in which only *one* species occurs. (N.B.— It is important to notice that this is not necessarily the *same* species for all these localities).

Between contour-lines 2 and 3 will lie all those localities possessing *two* species (again, not necessarily the *same* two species). And so on. Finally, the *n*th or highest contour-line will be either a closed oval, or possibly a series of closed ovals, of comparatively small extent, enclosing those few localities in which the highest total of *n* species occurs (again, be it noted, not necessarily the *same n* species in every locality within an oval).

Where the records are not sufficient, continuity or discontinuity may be assumed provisionally according to the evidence available. To give an example :—A species may be recorded from Sydney, Newcastle, Richmond River, Tweed Heads, Brisbane, Rockhampton. In such a case, it may reasonably be assumed that it occurs along the whole coast-line from Sydney to Rockhampton, because the conditions known to exist between these points naturally suggest its occurrence throughout. But,

suppose a species is recorded from Perth, Bunbury, Busselton, Albany, Adelaide, Port Elliott, Murray River. In this case, we might be justified in refusing to include the very barren coastal region along the Great Bight within the contour, until we had definite evidence of the occurrence there of the species in question.

Suppose, then, that the contour of the group, planned on the lines laid down, has been obtained. Of what value is it to us?

i. It is a *density*-contour for the group, but not an actual *species*-contour. It takes account only of the *number* of species occurring at a given point, not of the *actual* species comprising that number.

ii. It is not accurate in detail, but only *in broad outline*.

If these two facts be continually borne in mind, the contour may be used with very real value. The objects to be aimed at in using such a contour are as follows:—

1. To obtain on a single map a fairly accurate *graphical representation* of the present distribution of a group.

The author claims that the single "contour-map" will give to the mind *a clear and sufficiently accurate* representation of the distribution of the group, which *cannot be attained* by the perusal of many separate maps, on each of which the area of distribution of a single species of the group is mapped separately.

2. By comparison of the Specific Contours of many groups over the same region, these groups may be arranged into separate sets, each set possessing a contour *referable to a single type*, but not, of course, similar in details.

3. By a study of the different types obtained, the sum total of the fauna or flora of the region may be clearly visualised, and its different components clearly distinguished.

4. In many cases, valuable phylogenetic evidence may be deducible from a study of the contour.

Before dealing more fully with these points, it is necessary to consider (*a*) the general structure of a contour, (*b*) the general theory of contour-types.

### A. *The general structure of a contour.*

It is evident that, *in general*, the lowest contour-lines will enclose the largest areas, while, as the number-value of the contour-line increases, the area it encloses will become smaller and smaller.    Finally, the *n*th, or highest, contour-line will enclose a small area or series of areas surrounded by all the other contour-lines.    Such an area, representing a "summit" of the contours, may be spoken of as a *Zoocentre* ; it being clearly understood that in using this term no definite claim is put forward that the area is also *a centre of origin* for the group. The *Zoocentre* may be defined as the *centre of present greatest density* for the group.    It may be also a centre of origin, but in most cases it is possible that such a claim cannot be maintained for it.    Sometimes the area of the zoocentre is elongated very much in comparison with its breadth; it may then be termed the *Zoocentric Axis* of the group.    In the case where the contour exhibits more than one separate zoocentre, that which contains the highest number of species may be called the *primary* zoocentre, while those of lower value may be called *secondary* zoocentres.

It sometimes happens that the order of the contours is reversed, so that the higher contours enclose the lower, until in the middle may be found a small area in which perhaps only 2, 1, or even *no* species occur.    (Such a case, for example, is furnished by the failure of a subtropical group to ascend a central mountain range, though it may be spread abundantly all round it.    As one reaches a higher elevation, the number of species found will diminish; until, perhaps, above a certain level no species of the group will occur).    In such a case, the area of lowest contour may be called a *Lacuna*.    The mapping of lacunæ may be of the very greatest importance in the study of a group.

In constructing a contour, it is very important to leave out of account *purely local discontinuity*.    To give an exaggerated example : — Certain species of rush occur throughout Central Australia, *wherever there is a waterhole*.    The waterholes may be fifty or a hundred miles apart.    Nevertheless, the correct contour

needed for general study of this group of rushes should be drawn completely around the whole region in which they occur, and not as a number of small circles around the various waterholes. So, also, in mapping contours for groups of *Odonata*, we do not draw our contours along the boundaries of rivers and lakes, though the species are *actually* confined to them; rather, we include the whole area in which, *given the necessary water*, the particular species can be shown to occur.

### B. *The general theory of Specific Contours.*

Let us select for study a region, Z, separated by a definite barrier from another region, Y. A group of species occurring in Z may either have originated in Z, or they may have immigrated into it from some other region. Suppose a group of species, A, to have been inhabitants of the region Y at some past time before the barrier between Y and Z was effective, and let A be a dominant or increasing group. As it extends its boundaries, first one and then another species may reach Z and penetrate further and further into the new region. As these new arrivals encounter new conditions of life, such as altered temperature, rainfall, geological or vegetational conditions, their progress may be gradually stopped. Some forms may penetrate further than others, or may take different paths. As long as the barrier between Y and Z is not a *complete* one, so long will this immigration stream flourish and be clearly recognisable as such.

The contour of such an immigration group over the area Z is easily recognisable (Transparency 1) by the fact that its *zoocentre* either lies entirely outside or only partly inside the region Z, while the lower contour-lines extend farther and farther into the region.

For such a contour, the name *Ectogenic Contour* is proposed.

Suppose, next, that the barrier between Y and Z becomes complete, so that the immigrant-stream is cut off from the parent group. If it does not die out, it will gradually assimilate itself to the new conditions, *forming new zoocentres in those areas where conditions are most favourable to it.* After a sufficient interval of time, it will have evolved a group very distinct from

the parent group in Y, and the differences may be accentuated by the evolution of the two groups along divergent lines. Thus the group in Z gradually takes on a distinct or regional form, and becomes part of the native or autochthonous fauna of the region. We thus obtain a group *whose group-characters, as now recognised, were actually evolved within the region Z. Such groups form the characteristic fauna or flora of a given region,* and it is on the evidence of such groups that regional distinctions are based. Their contours are recognisable by the fact that their zoocentres lie *within* the region, while the lower contour-lines spread out farther and farther around, and may even overlap into surrounding regions (Transparency 2).

For a contour of this type, the name *Entogenic Contour* is proposed.

We can now go one stage further, and assume that a particular *entogenic* group in Z is faced with newer and stronger invasions of ectogenic groups from other regions, due, perhaps, to the removal of old barriers. In the struggle for existence, the older group will go under, and, if it is preserved at all, will appear as a remnant in one or more areas of the region Z. These areas *may* be the original zoocentres of its former entogenic contour; for it is reasonable to suppose that the group would be able to hold out longest in those areas where its density is greatest. They may, however, be simply "refuge" areas into which the remnants have been driven, and, in such cases, will not afford any evidence of the position of the original entogenic zoocentres. The contour of the group will now appear as a series of discontinuous ovals with no contour-lines of high value.

Such a contour may be termed a *Palæogenic Contour.* These are the contours of archaic groups. They may be sufficiently numerous to furnish part of the distinctive character of the fauna or flora of the region, but are usually of less importance, though not necessarily of less interest, than the entogenic and ectogenic groups of the region. Owing to the great changes in land distribution throughout long geological epochs, true palæogenic contours may very often be, and indeed usually are, *discontinuous over more than one region.* Hence their contours should be

mapped out on a complete map of the world, and then studied in relation to all the regions in which they occur. In those cases in which they occur in only one region, they may be very similar to entogenic contours, but will exhibit less density and extent.

We may now define the three main types of contour as follows :—

i. *Ectogenic Contours.*—The contours exhibited by groups which evolved their present group-centres *outside* the region Z, but have since invaded Z and form a definite part of its fauna and flora. The zoocentres will be either completely outside Z, or only slightly projecting into it, while the lower contour-lines will extend farther and farther into Z.

Generally, it will be found that the *species* forming the immigrant group are quite distinct from the main body of the group still located in Y. Very often they are also generically distinct, but the closer connection between the parent genus and its offshoots will still be evident, and will necessitate the two being taken together as a natural group, according to the rule already laid down.

ii. *Entogenic Contours.*—The contours exhibited by groups which evolved their present group-characters *within* the region Z. The zoocentres will lie entirely within Z, while the lines of lower contour will spread out more and more over the region, and one or more of them may possibly pass outside the region (forming the beginning of a new *ectogenic* contour for some other region).

Groups with entogenic contours are essentially those that give the distinctive character to a region, and on them the main zoogeographical regions of the earth are based.

iii. *Palæogenic Contours.* - The contours exhibited by groups which are remnants of what were once far more widely spread groups. Such contours may consist of one or more isolated areas of low value, and usually exhibit discontinuity over more than one region. These isolated areas may be regarded as the "sunken peaks" (probably the zoocentres) of a once large and continuous contour (just as an archipelago shows only the sunken peaks of what once formed a continuous land-mass).

It should be clearly recognised that these three types of contour are definitely connected, and that intermediate forms

may occur; for instance, an *ectogenic* group may have spread nearly all over a region, forming one or more secondary zoocentres in it, and still exhibit connection with the parent group, *entogenic* in a neighbouring region. As soon as that connection is definitely broken, and the offshoot assumes its own distinguishing charac- teristics, it becomes entogenic in the region of which it has taken possession. Again, an entogenic group may gradually die out, and so reach a stage at which it exhibits a contour intermediate between an entogenic and a palæogenic one. Such a contour would not, perhaps, show any discontinuity, but the paucity of contour-lines would indicate how very little more reduction was needed to produce a typical palæogenic contour.

It may be seen, also, how every group, in the course of time, from its rise to its final extinction, may go through the three stages of ectogenic, entogenic, and finally palæogenic contour in any given region,

Contours may exhibit flatness (in the case of groups with few species) or steepness (in the case of groups with many species in a small area). Several contour-lines may lie together in one single line, as, for example, along the coast-line of a region, or, in the case of several plant-feeding species which extend all together to the utmost boundary of distribution of a single food-plant. In such cases, it is probably best to exhibit the contours as a set of close parallel curves arranged in the order in which they would naturally come if the species did not end off quite coterminously. In the case of a coast-line, these parallel lines may be drawn on the map, actually over that part representing the sea, following the coast-line in general direction, but not its irregularities. (See the ectogenic contour in Transparency 1). Where the same species occurs in a number of islands, a single contour-line may be drawn round all the islands.

When the contours of different groups have to be studied in relation to the rainfall, temperature, or geological conditions of the region, they should be drawn on transparent paper, so that they can be placed over a map of the isohyets, isothermals, or geology of the region, as the case may be. This has been done in the Plate given with this paper, the printed map showing isohyets.

Application of the Method to a Selected Region.

Let us now take the Australian region and apply the method of specific contours to it, as far as our records will allow us. Probably no region has been so little worked; so that, if we are able to obtain satisfactory results from somewhat meagre records, we should be encouraged to expect even better results in regions where the records are more complete.

The groups will be selected from the *Odonata*, in which the author has collected fairly complete records during the past nine years.    Our objects will be (1) to recognise which groups of *Odonata* present ectogenic, entogenic, or palæogenic contours respectively; (2) to try to discover whether distinct subtypes exist within any of these three types.

By reference to the map in the Plate, it will be seen that some of the Papuan portion, and much of the Polynesian portion, has been omitted from the Australian region.    The records of the Papuan portion are not complete enough, while the contours exhibited do not in any case extend into that part of the Polynesian subregion omitted.    Owing to the small size of the map, the inland continental limits of the various contour-lines have been somewhat extended, otherwise they would appear too closely crowded along the coast-line to be distinguishable on so small a scale.

A. *Ectogenic Contours.*—Transparency 1 exhibits the approximate specific contour of the genus *Rhyothemis*.    This is a genus of dragonflies with coloured wings, belonging to the subfamily *Libellulinæ*, and very distinct from its nearest allies.    It is entogenic in the Oriental region, but has spread eastwards across Wallace's line, appearing as a strong immigration stream into the Papuan subregion and along the northern and north-eastern coasts of Australia.    One species (*R. graphiptera*) has spread as far south as the Clarence River, in New South Wales, and reaches also inland up to the 3,000 feet level in North Queensland. Another (*R. phyllis chloë*) reaches just into New South Wales at Murwillumbah, and does not extend as far inland as *R. graphiptera*.    A third (*R. chalcoptilon*) has not been recorded south of Gayndah.    Two other species (*R. resplendens* and *R. braganza*) are

only found very much further north, the former extending from Papua to Cairns, the latter from Cape York to Townsville. The resulting contour exhibits a typical *ectogenic* arrangement, the zoocentre containing five species and lying so as just to intrude into the northern part of Australia.

Other genera of *Odonata* exhibiting a contour similar to this in general form (not, of course, similar in actual detail or density) are :—

*Agrionoptera, Macromia, Ictinus, Anax, Gynacantha,* the group comprising the closely allied Australian genera of the legion *Protoneura, Pseudagrion, Argiocnemis, Agriocnemis. Austrolestes,* as an offshoot of the cosmopolitan *Lestes,* still very little differentiated from the parent stock, exhibits, in Australia, a very interesting contour intermediate between typical ectogenic and entogenic form. It is, in fact, just in process of being " budded " or separated off from the parent stock.

A certain amount of evidence goes to show that small invasions from the Oriental region have reached Australia by way of Timor. My records are not, however, complete enough to present a contour of this type for any group of *Odonata,* though I have little doubt that such could be established as a result of careful collecting in the North-West.

We see, therefore, the probability of two distinct kinds of ectogenic contour in Australia. For these I propose the names *Torresian* and *Timorean* respectively, indicating the respective paths by which the stream of immigration reached Australia.

B. *Entogenic Contours.* —Transparency 2 exhibits the contour of the group *Synthemina,* comprising the closely allied genera *Synthemis, Metathemis,* and *Choristhemis.* This group belongs to the subfamily *Corduliinæ,* and has no near allies. The contour shown is typical of the greater portion of the essentially Australian fauna. It consists of two separate portions in which the species are more or less differentiated from one another. A large area is occupied on the east, extending from New Guinea to Tasmania, while on the west the genus reappears in the south-western corner of Australia. The separation of the two

areas has clearly been brought about by the destruction of the group in the dry area of country along and north of the Great Bight—the Desert Barrier between East and West Australia. The species of *Synthemina* found in Western Australia are all specifically distinct from those in the East, except *S. macrostigma*, which is only differentiated into the two closely allied subspecific forms *occidentalis* and *orientalis*.    This species also occurs, somewhat remarkably, in Fiji.

The primary zoocentre of this contour is along the highlands of South-eastern Australia, while a secondary zoocentre is developed around Cape Leeuwin.

In many genera of animals not so dependent on the rainfall as are the *Odonata*, this same form of contour is exhibited, but the lower contour-lines of the eastern portion will lie *very much farther inland* to the west, and in many cases one or more species may occur across the Desert Barrier, thus linking up the two portions of the contour into one complete whole.

Other genera of *Odonata* exhibiting this contour are :—*Austrogomphus, Austroæschna, Hemicordulia* (in which the western species also occur in the east, and may be linked up with them when sufficient records are available).

To a contour of this type I propose to give the name *Holonotian*, further distinguishing the two portions as the *Eonotian* on the east, and the *Hesperonotian* on the west.    The genus *Diphlebia* exhibits an *Eonotian* contour only, being completely absent from the South-West.    Many genera in other groups of animals can be shown to exhibit Eonotian contours; but, so far, the only purely *Hesperonotian* contours known are exhibited by certain genera of plants peculiar to the South-West.

The commonest form of Holonotian contour is one in which the primary zoocentre tends to be located most strongly in the south-east of the continent, though it may run northwards for a considerable distance as a narrow *zoocentric axis*.    Sometimes two distinct zoocentres may occur, one in the south-east, and one near the border-line between New South Wales and Queensland. In nearly all those cases where the zoocentre tends to be in the south-east, one or more of the contour-lines will extend over

Tasmania; but it is rather the exception than the rule for any of these contour-lines to reach into New Guinea. In the *Odonata*, the group *Synthemina* is the only one known to me whose contour embraces both Tasmania and New Guinea.

Another variation of the Holonotian contour has a zoocentre tending to be located more northwards, usually in Northern New South Wales, or in South Queensland. In such cases, (e.g., *Diphlebia*) the contour may reach to New Guinea, but not into Tasmania, and generally does not exhibit any Hesperonotian portion.

Besides the Holonotian contour, representative of so many Australian groups, we find other types of entogenic contours. Unfortunately, the records available are not sufficient for the actual construction of these contours, but only sufficient to indicate broadly their existence. One of these may be termed the *Papuan* contour, and has its primary zoocentre located in Papua. The lower contour-lines spread out over the surrounding islands, and also down into Queensland, that portion of the contour appearing very similar to the ectogenic *Torresian* contour already defined — in fact, a group with Papuan contour may rightly be considered as entogenic in Papua, but ectogenic in Queensland, if it is desired to contrast the fauna of Papua with that of Australia proper. Again, in the case of strong-flying insects, one or more of the outermost contour-lines may reach beyond Wallace's line into the Oriental Region proper, and especially into Celebes, which appears to be a kind of link between the two regions, receiving both Oriental and Australian forms.

In the *Odonata*, the genus *Argiolestes* has a Papuan contour. There are a large number of species in Papua, and probably many more to be discovered. One species, at least, reaches to the Celebes. This group has, however, extended down into Australia itself far more vigorously than would be usually expected in the case of a tropical group, and is actually in pro-cess of budding off a distinct Holonotian contour, having a secondary zoocentre in Northern New South Wales with five species; and also a single species occurring in Western Australia.

A more typical Papuan contour is exhibited by the well-known *Ornithoptera*-group of the *Papilionidæ*. The species of this group spread out from Papua as a centre, and a comparatively small branch extends into Australia itself, one species reaching as far south as the Richmond River in New South Wales.

Another form of entogenic contour, not, so far, found amongst the *Odonata*, appears to be shown by the distribution of the Australian fresh-water Crayfish, in which zoocentres of low numerical value occur in the North, South-East, and South-West of the continent respectively. With sufficient records, it seems that this contour would appear as the clear result of *radial* distribution in three separate directions from the large central lake known to have existed in Australia in Cretaceous time. It might, therefore, be suitably called a *Radial Contour*.

The study of entogenic Australian groups occurring in Tasmania, and the careful contouring of their separate distributions, may be expected to throw some light on the question of Antarctic connections. The evidence afforded by the *Odonata*, so far, is not very strong, but the very close alliance between the species of the isolated group *Petalini*, found only in Chili and on the Blue Mountains, will be regarded by some students as one link in the chain of evidence for a former connection between Australia and America *viâ* Antarctica. If the Blue Mountain species exists also in Tasmania, the argument will be much strengthened. The fact that it has not yet been recorded is of little value, when we consider how many years it has taken to secure only four specimens in a well collected locality close to Sydney.

C. *Palæogenic Contours.*—Transparency 3 exhibits part of the contour of the subfamily *Petalurinæ*, a small group of *Odonata* with no near allies. In the Australian region, it is represented by the genus *Petalura* in Australia, and by *Uropetala* in New Zealand. *Petalura gigantea* occurs in the Blue Mountains and their southern spurs, and also on Stradbroke Island, South Queensland. *P. ingentissima* is confined to Kuranda and Herberton, North Queensland, while *P. pulcherrima* extends from Kuranda to Cooktown. *Uropetala carovei* is common in the

North Island of New Zealand. In Chili, the group is repre-
sented by *Phenes raptor*, and in North America by *Tachopteryx
thoreyi* in the State of New York, and by *T. hageni* in Nebraska.

This contour, therefore, is seen to be discontinuous over three
separate regions, the Australian, Neotropical, and Nearctic.
Such a contour, as is well known, can only be exhibited by
archaic groups, and is only explicable on the supposition that it
represents the remains of a once much more complete and wide-
spread contour over several regions. One of the best known
examples is that of the *Dipnoi*.

In *Odonata*, a further example of a palæogenic contour is
exhibited by the group *Petalini* of the *Æschninæ*, mentioned
above, with one species on the Blue Mountains, and six in Chili.

Contours exhibiting the passage from the entogenic type to
the discontinuous palæogenic type are not infrequent. Such, for
instance, amongst the *Odonata*, are probably those of the genera
*Nannophya* and *Nannophlebia*; while the *Monotremata* furnish
an excellent example that will be more clearly appreciated.

We may now exhibit the various types of contour for the
Australian region as follows, bracketing those that are not fully
established.

| Type. | Subtype. | Examples. |
|---|---|---|
| A. ECTOGENIC... | A₁ TORRESIAN ......<br>[A₂ TIMOREAN] | *Rhyothemis, Agrionoptera, Gyna-cantha*, &c. |
| (Transference from A to B :—*Austrolestes*.) | | |
| B. ENTOGENIC.. | B₁ HOLONOTIAN......<br>$\{b_1$ Eonotian ......<br>$\{b_2$ Hesperonotian<br>B₂ PAPUAN ... .....<br>[B₃ RADIAL] | *Synthemina, Austroæschna*, &c.<br>*Diphlebia*.<br><br>*Argiolestes*. |
| (Transference from B to C :—*Nannophya, Nannophlebia*.) | | |
| C. PALÆOGENIC | | *Petalurinæ, Petalini*. |

4

## The composition of a Regional Fauna.

One of the great advantages of the method of Specific Contours is that it clearly separates out the different types or "layers," as it were, which make up the fauna of any given region. The attempts to subdivide regions into definite subregions do not give sufficient prominence to this, but tend rather to give an idea of essential differences between the divisions, separated by hard and fast lines. The method of Specific Contours may be called a *three-colour process*, in which the true "colour" or appearance of any given fauna is obtained by the superposition of separate plates on which the three different distributions, ectogenic, entogenic, and palæogenic, are drawn. Only by such an analytical process can we obtain a clear idea of the changes in the faunal character of different parts of a region.

To take a good example of this :—The North Queensland coastline does not strike the visitor as typically Australian in either its fauna or flora. Yet if these be analysed, the very strong entogenic element very soon becomes apparent, and the overlying ectogenic element which marks it can be differentiated out as of Oriental origin. As soon as one gets inland, the effect of the ectogenic element becomes much less marked, and the entogenic fauna and flora show up very distinctly. As one travels southwards, the effect of the ectogenic element diminishes.

Again, on the Blue Mountains, there is at once apparent a very strongly marked entogenic fauna and flora. Almost lost in this, but still present—and, by its presence, adding to the variety and interest of the fauna—we distinguish the remains of palæogenic groups whose value to the phylogenist can scarcely be over-estimated.

## The factors of zoogeographical distribution.

Different students of zoogeography have given prominence to various factors which have brought about the present distribution of the fauna and flora of the earth. It is necessary, however, to distinguish clearly between the two classes of factors which contribute to the result. They may be classed as follows :

i. *Primary Factors.*—Those which determine the presence or absence of groups in the fauna or flora of a region. These factors

are : —(a) the position and extent of the region with reference to the centres of origin of the various groups; (b) barriers.

ii. *Secondary Factors.*—Those which determine the form of contour exhibited in a region by a group whose presence has been brought about by the action of i. These are :—(a) climate (rainfall, temperature); (b) the geology of the region; (c) the strength of the tendency to vary or mutate exhibited by the group in question; (d) further alteration in the position of barriers, after the arrival of the group within the region.

In determining the distribution of the Australian *Odonata*, the primary causes have been—(a) The proximity of the Australian region to the Oriental. (b) The inefficiency of Wallace's line as a barrier to strong-flying species. (c) The " bridges " across Torres Straits and Timor, allowing of definite streams of immigration. (d) Possible lost connections with Antarctica and thence with South America.

The secondary causes, which have restricted the spread of the group within the Australian continent, have been—(a) The restriction of the rainfall mainly to the coastal districts. (b) The Desert Barrier between South-East and South-West Australia. (c) The Bassian Barrier between Tasmania and the mainland. (d) The changes in mean temperature as we pass from north to south.

Of these, the distribution of the rainfall is, no doubt, the controlling factor in determining the narrow form of the Holonotian contours exhibited by Australian *Odonate*-groups. Entogenic groups of insects of other orders, less dependent upon the rainfall, exhibit Holonotian contours of very much greater width.

The subdivision of Holonotian contours into Eonotian and Hesperonotian portions has been brought about by the Desert Barrier.

The absence of certain forms from Tasmania which occur commonly on the mainland at the points nearest to the island, can only be explained by the supposition that these forms arrived at their south-eastern limit after the Bassian Isthmus had sunk beneath the sea. This affords valuable evidence of the relative

archaism of (*a*) *Austrothemis* and *Nannophya* (present in Tas-
mania) as compared with *Diplacodes* (absent).    (*b*) *Procordulia*
(present) compared with *Hemicordulia* (absent except for new
colonisation by *H. tau*, a species with strong migratory tenden-
cies).    (*c*) *Æschna* (present) compared with *Anax* (absent).

The lowering of the mean temperature as we pass southwards
down the eastern coast-line is the chief factor in restricting the
ectogenic invasion of groups of Oriental origin.    As far as the
northern rivers of New South Wales, the mean temperatures are
very high, the influence of Antarctic depressions and southerly
winds being very little felt.    To this limit many essentially
tropical groups, such as *Rhyothemis*, have penetrated.    Some few
reach to Sydney and beyond; but, as we go south, the number
diminishes very rapidly, and the ectogenic element soon dis-
appears.    A similar process, no doubt, affects the composition of
the *Odonate* fauna of the western coast-line, about which very
little is known.    Around Perth, only *Tramea* and *Pantala* have
been noticed as of ectogenic origin.

In the Plate, the isohyets or lines of equal rainfall are given
as supplied by the Federal Meteorological Bureau.    In the
northern portion of the continent, this rainfall is almost wholly
of monsoonal origin, and falls mainly during summer (December
to March).    In the South-West and South-East, and in Tas-
mania, the rainfall is mostly of Antarctic origin, and falls mainly
in the winter (May to September).    In New South Wales, both
monsoonal and Antarctic influences are at work, with the result
that both summer and winter may be dry or wet according to the
intensities of the two operating factors.    It will readily be seen
from the map and transparencies that—(*a*) Ectogenic groups
exhibit contours broadly similar to the contours of the monsoonal
isohyets.    (*b*) Entogenic groups (Holonotian) exhibit contours
more dependent upon the distribution of Antarctic rainfall.

This correlation between specific contour and rainfall is in no
way a complete one.    Above a certain amount, rainfall may tend
to retard the spread of a group.    The west coast of Tasmania,
with a rainfall up to 100 inches a year, appears to be very poor
in *Odonata*; doubtless owing to its sunless and cold summer.

The excessively wet portion of tropical coast-line centred around
Innisfail, North Queensland, with a rainfall up to 130 inches a
year (nearly all summer rain) is not so rich in species as the sur-
rounding districts with from 50 to 70 inches.

## Other Applications of the Method.

The Method of Specific Contours may be profitably used in
studying the density distribution of Zonal Groups—*i.e.*, groups
which are not confined to one zoogeographical region, but are
distributed along a zone of the earth's surface. On the map of
the world (Mercator's projection) contours may be shown of
Boreal, Holarctic, Bipolar, or Circumtropical groups which will
present at a glance the salient features of distribution in a graphic
manner. The author has worked out on these lines the contour
of the holarctic genus *Sematochlora* with a very satisfactory
result, though the number of detailed records available was
scarcely sufficient to give a very accurate contour. Leaving out
of account three species usually included in the genus (two from
New Zealand and one from Chili) about whose inclusion in the
genus there is ground for doubt, we obtain a contour of the zonal
type ranging round the northern temperate zone. It is interrupted
by the Atlantic—as might be expected—but not by the Pacific,
since two species, at least, occur on both sides of Behring's
Straits, and extend far westwards into Siberia and eastwards
into Canada. The primary zoocentre seemed to be located in
the vicinity of the State of Maine, U.S.A., with a density of six
species, while a secondary zoocentre of large extent but of less
density (three) runs across the northern part of Europe and
Asia. The boundary line of the contour southward throws out
two well-defined projections into lower latitudes, one down along
the eastern coast of U.S.A. as far as Florida, another into Japan,
while a somewhat indefinite bulging takes place to include
records of a single species extending into Arizona.

This contour is not published here, because the inequality of
the records available scarcely admits of its consideration in any-
thing but the broadest of aspects. More collecting has been
done in the one State of Maine than in the whole of Siberia.

The apparent zoocentre in Maine may be, therefore, only due to
the completeness of the local records, and the genus may possibly
attain as great, or even greater, density in some part of Siberia.
Generally speaking, the number of records necessary for drawing
an approximate contour in the case of a zonal group will be much
higher than in the case of a regional group, since the former will
extend into at least two regions.

Other examples of zonal distribution in *Odonata* whose dis-
tribution might be advantageously studied by this method are :—

Holarctic—*Libellula, Sympetrum, Leucorrhinia, Gomphus,
Boyeria, Calopteryx.*

Circumtropic—*Macromia, Tramea, Gynacantha, Teinobasis.*

In the study of zonal groups, the contour itself will decide in
what region or regions a given zonal group may be considered to
be entogenic; viz., those regions in which that group can be seen
to have established definite zoocentres.  For example, the genus
*Somatochlora* may be rightly considered entogenic in the Nearctic
Region, and also (though apparently not so definitely) in the
Palæarctic Region.  Other zonal groups are quite clearly ento-
genic in one region but ectogenic in another.  *Tramea*, for
instance, appears to be entogenic in the Neotropic Region, with
an ectogenic outgrowth into the Nearctic Region and another
into the Australian Region.

Cosmopolitan groups, such as *Anax, Æschna, Lestes*, may also
be studied by this method; but, of course, the number of records
necessary for the complete contouring of such a group will be
even greater than in the case of a zonal group.

The method may also be applied to the study of a *barrier*, in
the following manner :—A map should be taken showing the
barrier, with parts of the surrounding regions, and over this map
the partial contours of various groups, drawn on transparencies,
may be placed in turn.  The efficacy of the barrier may be gauged
by considering the percentage of contours showing *total discon-
tinuity* across the barrier.  In so far as group contours are com-
pletely delimited or cut off by the barrier (*i.e.*, the group is pre-
vented from passing across the barrier at all), the barrier may be
considered a *Primary Barrier*; but, in so far as group contours

are only *severed* by it, (*i.e.*, the group is divided into two distinct portions) the barrier is only a *Secondary Barrier*. It is clear that a barrier can only be a Primary Barrier to those groups whose arrival in its neighbourhood is of later date than the uprising of the barrier; while, even to such groups, if they possess special facilities for passing the barrier, it may only play the part of a Secondary Barrier, or even be no barrier at all. On the other hand, if the date of the uprising of the barrier be later than that of the arrival of the group, it cannot rank higher than as a Secondary Barrier. A recognised barrier, such as Wallace's line, might be carefully treated in this manner for a large number of groups with very valuable results.

A further suggestion as to a valuable use of this contour method is offered by the author for the case of migrating groups of birds. With sufficient records, two separate contour maps might be drawn up for, say, one of the genera of the *Fringillidæ*, showing (*a*) the contour of the group during the nesting season; (*b*) its contour during the winter. These two contours, drawn on large maps and exhibited side by side, would bring home to us, more clearly than pages of records, the movements of the group during the changing seasons of the year. Probably the records available in Europe and America for such a contour will be found to be quite sufficient.

In conclusion, the author contends that the study of zoogeo- graphical distribution will be advanced by the method outlined in this paper, and that contours of groups are a more natural unit for study than theoretical subdivisions of regions into separate portions.